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Ecosystem carbon exchange in two terrestrial ecosystem mesocosms under changing atmospheric CO_2 concentrations

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Abstract The ecosystem-level carbon uptake and respiration were measured under different CO_2 concentrations in the tropical rainforest and the coastal desert of Biosphere 2, a large enclosed facility. When the mesocosms were sealed and subjected to step-wise changes in atmospheric CO_2 between daily means of 450 and 900 μmol mol^{-1}, net ecosystem exchange (NEE) of CO_2 was derived using the diurnal changes in atmospheric CO_2 concentrations. The step-wise CO_2 treatment was effectively replicated as indicated by the high repeatability of NEE measurements under similar CO_2 concentrations over a 12-week period. In the rainforest mesocosm, daily NEE was increased significantly by the high CO_2 treatments because of much higher enhancement of canopy CO_2 assimilation relative to the increase in the nighttime ecosystem respiration under high CO_2. Furthermore, the response of daytime NEE to increasing atmospheric CO_2 in this mesocosm was not linear, with a saturation concentration of 750 μmol mol^{-1}. In the desert mesocosm, a combination of a reduction in ecosystem respiration and a small increase in canopy CO_2 assimilation in the high CO_2 treatments also enhanced daily NEE. Although soil respiration was not affected by the short-term change in atmospheric CO_2 in either mesocosm, plant dark respiration was increased significantly by the high CO_2 treatments in the rainforest mesocosm while the opposite was found in the desert mesocosm. The high CO_2 treatments increased the ecosystem light compensation points in both mesocosms. High CO_2 significantly increased ecosystem radiation use efficiency in the rainforest mesocosm, but had a much smaller effect in the desert mesocosm. The desert mesocosm showed much lower absolute response in NEE to atmospheric CO_2 than the rainforest mesocosm, probably because of the presence of C_4 plants. This study illustrates the importance of large-scale experimental research in the study of complex global change issues.

Key words Atmospheric CO_2 · Canopy photosynthesis · Coastal desert · Net ecosystem exchange · Tropical rainforest

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Introduction

Although many studies have demonstrated that northern temperate forests are likely the missing sink for atmospheric CO_2 (e.g., Wofsy et al. 1993; Ciais et al. 1995), there is increasing evidence for possible CO_2 sinks in several tropical ecosystems including introduced pastures in South America (Fisher et al. 1994), undisturbed tropical rainforests in Southwest Amazonia (Grace et al. 1995a, b), and native Brazilian cerrado (Miranda et al. 1997). These field studies demonstrated net carbon sequestration on an annual basis by tropical ecosystems regardless of the significant differences in soil conditions, species compositions, and primary productivity among these ecosystems. It has been hypothesized that fertilization as a result of increasing atmospheric CO_2 coupled with a higher deposition rate of nitrogen is the major process responsible for increased carbon uptake by terrestrial ecosystems (Körner 1993). Long-term monitoring of plots in mature humid tropical forests in South America revealed that biomass gain by tree

growth exceeded losses from tree death at most study sites, suggesting that Neotropical forests may be a significant carbon sink as a result of nutrient fertilization from increased CO_2, and increased N and P deposition (Phillips et al. 1998). However, experimental testing of this hypothesis at the ecosystem level in the field for the tropical ecosystems is technically challenging because of the large scale and high costs (Koch and Mooney 1996).

To date, ecosystem CO_2 experiments have focused mainly on Arctic and temperate ecosystems (Oechel et al. 1994; Drake et al. 1996; Pinter et al. 1996), and are still lacking in tropical ecosystems. Nevertheless, previous CO_2 enrichment experiments in terrestrial ecosystems have demonstrated that more productive systems have a higher absolute productivity increase in response to elevated CO_2 (see review by Koch and Mooney 1996). If this trend can be extended to tropical ecosystems in general, we can expect that tropical ecosystems should be potentially the most responsive to changing atmospheric CO_2. Without knowledge of how tropical ecosystems respond to increasing atmospheric CO_2, accurate predictions of the role of the terrestrial biosphere in future global carbon cycle will be limited (Körner 1996; Koch and Mooney 1996). The results presented here suggest that while the logistical problems of manipulating intact tropical ecosystems in the field may be insuperable, large scale experimental mesocosms can offer insights into ecosystem responses to increasing CO_2.

The effects of elevated CO_2 on photosynthesis and growth of tropical species, especially at their seedling stage, have been well studied now (e.g., Oberbauer et al. 1985; Reekie and Bazzaz 1989; Ziska et al. 1991), but the responses of tropical plants to elevated CO_2 may be quite different from those to be expected for ecosystem processes in the tropics (see review by Bazzaz 1990). Until CO_2 enrichment experiments of whole canopy in natural tropical ecosystems can be performed, investigations with laboratory experimental ecosystems provide an useful approach for assessing the CO_2 effects in highly structured ecosystems (Körner and Arnone 1992; Arnone and Körner 1995; Körner 1995; Lin et al. 1998). For example, Körner and his co-worker observed that canopy CO_2 uptake, fine root production, and soil respiration were increased under elevated CO_2, but there were no significant effects on net ecosystem carbon accumulation after several months of elevated CO_2 treatment in a laboratory rainforest microcosm (Körner and Arnone 1992; Arnone and Körner 1995). These studies pointed out the inadequacy of scaling-up from physiological baselines to ecosystem processes without accounting for interactions among components, and the urgent need for whole-system experimental approaches in global change research.

In this study, we investigated the effect of increasing atmospheric CO_2 on ecosystem carbon exchange in tropical/subtropical ecosystems during a summer period using the two terrestrial ecosystem mesocosms (the tropical rainforest and the coastal desert) of Biosphere 2, a large-scale enclosure facility. These subsystems of Biosphere 2 are of larger scale, with more taxonomic/structural diversity, much higher spatial heterogeneity, and much bigger physical size than most laboratory microcosms available so far for CO_2 enrichment research. Previous results using these mesocosms in the winter of 1995–1996 indicated that ecosystem gas exchange under different CO_2 concentrations can be measured directly and simulated with simple physiological models (Lin et al. 1998; Rosenthal et al., in press; Tubiello et al., in press). Here we extended this mesocosm approach by comparing the responses of two distinct terrestrial ecosystems to increased CO_2 concentration.

Materials and methods

Description of tropical rainforest and coastal desert mesocosms

Biosphere 2 is an enclosed apparatus comprised of large-scale synthetic communities representing rainforest, desert, savanna, and other ecosystems in the tropics and subtropics (Fig. 1). This 1.25-ha complex contains about 170,000 m^3 of atmosphere, 1.5 million l of freshwater, 3.8 million l of salt water, and 17,000 m^3 of soils (Nelson et al. 1993). The tropical rainforest and the coastal desert of Biosphere 2 represent two contrasting ecosystems, and both of them were established in 1990. The rainforest represents a humid tropical rainforest in southern America, while the desert mesocosm represents a coastal desert with low precipitation but high relative humidity in the Vizcaino region of Baja California. The main physical, edaphic, and biological characteristics of these mesocosms are listed in Table 1.

By the summer of 1996, the top canopy in the rainforest mesocosm had reached 11–12 m high and covered a wide area. Secondary canopy and understory plants had also established under or between big trees. The daily mean air temperature for this tropical mesocosm was set at 27°C (maximum 35°C, minimum 20°C), with relative humidity at about 85%. Due to thermal stratification in this mesocosm during the summer season, the canopy temperature occasionally reached 45°C or higher in the afternoon of hot sunny days.

In the coastal desert mesocosm, C_4 grasses and shrubs (about 40%, leaf area proportion), C_3 shrubs and trees (about 55%), and

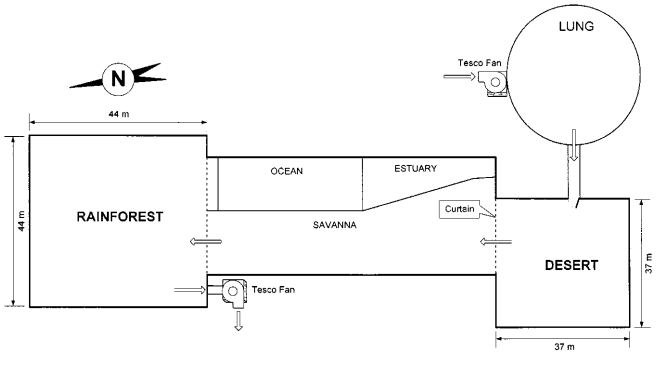

Fig. 1 Schematic diagram showing the five major mesocosms of Biosphere 2 and associated systems for internal pressure regulation (*lung*), air flow control (*Tesco fans*) and sub-system separation (*curtains*). The physical and biological features of the two mesocosms used in this study (the tropical *rainforest* and the coastal *desert*) are given in Table 1

Table 1 Physical, edaphic and biological characteristics for the two terrestrial mesocosms of Biosphere 2 used in this study

Characteristics	Tropical rainforest	Coastal desert
Vegetated area (m^2)	1,642	1,252
Height (m)	28	23
Soil volume (m^3)	6,000	4,000
Water volume (m^3)	400	100
Air volume (m^3)	25,400	16,600
Total volume (m^3)	35,000	22,000
Soil organic matter content (%)		
0–20 cm	4.16 ± 0.42	0.60 ± 0.14
40–60 cm	3.88 ± 0.39	0.34 ± 0.07
Soil C/N ratio		
0–20 cm	11.1 ± 0.7	31.9 ± 9.1
40–60 cm	12.3 ± 1.4	42.3 ± 14.4
Soil pH		
0–20 cm	7.68 ± 0.07	8.34 ± 0.18
40–60 cm	7.98 ± 0.10	8.50 ± 0.31
Dominant soil texture	Sandy clay loam	Clay, Sandy loam
Most common plant species	*Clitoria racemosa*[a] *Ceiba pentandra*[a,b] *Pterocarpus indicus*[b] *Arenga pinnata*[b] *Ceiba shrieberiana*[a,b] *Musa acuminata cv*[a] *Syngonium podophyllum*[a] *Alpinia zerumbet* *Epipremnum pinnatum*[a]	*Encelia ventorum*[a] *Nicotiana glauca*[a,b] *Trixis californica*[a,b] *Euphorbia xantii* *Pennisetum ciliare*[a] *Panicum maximum* *Encelia asperifolia*[b] *Atriplex* spp.[a,b] *Prosopis glandulosa*[b]
Total plant species (estimated):	70	100
Plant species density (species ha^{-1}):	362	730

[a] Sampled for foliar nutrient analyses
[b] Measured for predawn water potentials

CAM plants (about 5%) cover different soil zones. The leaf area index was estimated to be around 1.8 m^2 m^{-2} during the study period, using a LAI-2000 canopy analyzer (LI-COR, Lincoln, Neb., USA). The desert mesocosm was managed for active growth during the experimental period by adjusting precipitation and temperature. The mean daily air temperature for this mesocosm was maintained around 26°C (maximum 32°C, minimum 20°C), with monthly precipitation less than 25 mm applied as brief showers at intervals of 1 week. There was no obvious thermal stratification in the mesocosm because of air circulation above the vegetation canopy.

CO_2 control and treatments in summer 1996

As described previously, the special features of the Biosphere 2 systems preclude traditional replications of CO_2 treatment and control conditions (Lin et al. 1998). In this study, we used a time-series of step-wise changes in atmospheric CO_2 concentration to create the control (near ambient CO_2) and treatment (elevated CO_2) conditions as well for the replication (temporal replicates). Temporal gradients in CO_2 concentrations were created by controlled exchange of the elevated CO_2 air inside Biosphere 2 with outside ambient air using a fan system (Fig. 1). The outside ambient air was pushed first into the south lung, past the coastal desert mesocosm, and finally through the rainforest mesocosm before being drawn out of the structure by another fan near the northwest corner of the tropical rainforest mesocosm. By adjusting the flow rate and the duration of exchange, we could manipulate atmospheric CO_2 concentrations and maintain each level for several weeks.

In this study, the atmospheric CO_2 concentration was maintained at a "high" level (daily mean around 900 μmol mol^{-1}) for 4 weeks starting on 27 May, then at a "low" level (daily mean around 450 μmol mol^{-1}) for 4 weeks starting on 24 June, and then at the high level again for an additional 4 weeks starting on 22 July (Fig. 2). The atmospheric CO_2 concentrations in each mesocosm were measured with a LI-6262 CO_2/H_2O analyzer (LI-COR) at three locations representative of the major air space of each mesocosm. The CO_2 analyzers were calibrated periodically (every 2 h) using a custom-designed five point calibration system (Rosenthal et al., in press). The precision for the CO_2 concentration measurement was about ±1 ppm for most of time during this study.

During this 12-week experimental period, light level was measured at the canopy top with LI-190SA quantum sensors (LI-COR). The light data were smoothed using a running average technique to remove large variations in the values caused by the shadows of the space-frame structure. The daily mean and daily total photosynthetically active radiation (PAR) were then calculated using the smoothed data. The climate control systems of Biosphere 2 were used to maintain relatively constant temperature

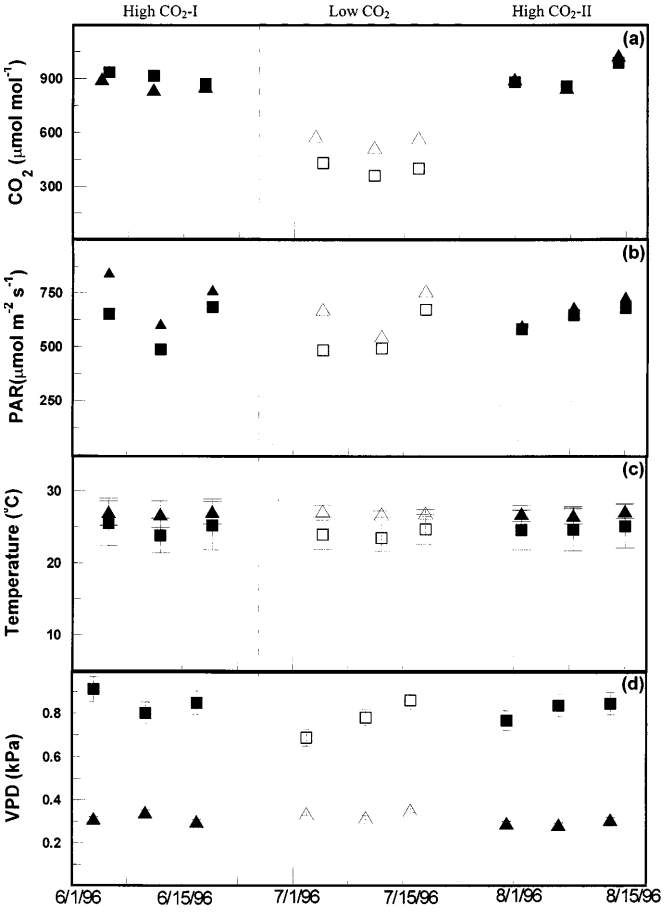

Fig. 2a–d Daily mean atmospheric CO_2 concentration, photosynthetically active radiation (PAR) at the canopy top, air temperature, and water vapor pressure deficit (VPD) in the tropical rainforest (triangles) and the coastal desert (squares) of Biosphere 2 during the summer of 1996 when the atmospheric CO_2 was controlled at a high level (*high CO_2-I, filled symbols*), a low level (*low CO_2, open symbols*), and then the high level again (*high CO_2-II, filled symbols*). PAR and CO_2 concentration were measured at two locations in each mesocosm, while air temperature and VPD were measured at three locations (mean ± SE)

and relative humidity throughout the entire experimental period (Fig. 2). The air and soil temperature, relative humidity, and barometric pressure were recorded continuously throughout the experimental period.

To characterize the pH and nutrient status for the mesocosms during the experimental period, we collected surface soils (0–20 cm) from five representative locations, and fully expanded leaves from five dominant plant species (see Table 1 for the species list) at the beginning of each CO_2 treatment phase. The soil and leaf samples were first dried at 70°C for 48–72 h and then ground to ensure sample homogeneity. The soil samples were then analyzed for soluble nitrate, phosphate, potassium, and ferric iron, and the leaf samples were analyzed for total N, P, K, Ca, Mg and Fe contents. All nutrient analyses were performed by the Soil and Water Analysis Laboratory at Colorado State University in Fort Collins, Colorado, United States.

During the entire experimental period, rain events were carefully scheduled to ensure stable soil moisture over the experimental period (in the rainforest), and to be similar at the beginning of each CO_2 treatment phase (in both the rainforest and the coastal desert). For the rainforest mesocosm, simulated rains were always delivered on Mondays and Fridays. For the desert mesocosm, rains were delivered at the beginning and middle of each 4-week CO_2 treatment phase. To monitor possible changes in water availability for plant uptake during the experimental period, we measured predawn water potentials for the five or six dominant species in each mesocosm with a PMS-1003 pressure chamber (PMS, Corvallis, Ore., USA). These measurements were made between 3:00 and 5:00 a.m. local time.

Measurements of ecosystem carbon exchanges

After each CO_2 concentration had been maintained for about 1 week, each mesocosm was temporarily sealed for periods of 48 h by deployable polyethene curtains. During each closure period, SF_6 was released and the change in its concentration after release was monitored using a HP 5890 II Gas Chromatograph (HP, San Diego, Calif., USA) to determine the overall leak rate across the partition curtains. The diurnal change in atmospheric CO_2 concentration within each mesocosm during the first 24 h for each closure period was used to calculate the net ecosystem exchange (NEE) of CO_2 at intervals of 15 min. We did not use the data from the 2nd day of closure since atmospheric CO_2 concentration was altered by the 1st day of closure. Within a closed mesocosm of Biosphere 2, the CO_2 budget could be described as follows:

$$\mathrm{NEE} = -\mathrm{d}[\mathrm{CO_2}]_a/\mathrm{d}t \times M_a - F_{leak} - F_{conc}$$

where $\mathrm{d}[\mathrm{CO_2}]_a/\mathrm{d}t$ is the rate of change in CO_2 concentration in the air inside a closed mesocosm, M_a is the number of moles of air within the mesocosm, F_{leak} represents the CO_2 flux from the closed mesocosm to its neighboring one (i.e., the savanna, see Fig. 1) due to air leak through the partition curtains, and F_{conc} is the rate of CO_2 uptake by the concrete structure due to the carbonation reaction between CO_2 and calcium oxide (Severinghaus et al. 1994). All fluxes are expressed as μmol CO_2 per m^2 ground area per second. F_{leak} was estimated using the leak rate (around 1–2% h^{-1}) and the gradient in atmospheric CO_2 concentration across the curtains. F_{conc} depends primarily on the CO_2 concentration of Biosphere 2 air and the diffusivity of CO_2 in the concrete, and was estimated as described previously (Severinghaus et al. 1994). It has been demonstrated in a previous trial experiment that F_{leak} and F_{conc} account for only a few percent of the change in $\mathrm{d}[\mathrm{CO_2}]_a/\mathrm{d}t$ and have a negligible effect on calculated NEE (Rosenthal et al., in press). Thus, the errors associated with these estimations should not cause any significant effect on NEE. Here net uptake of CO_2 by the mesocosm is denoted by positive NEE values, while negative NEE values represent the net release of CO_2 to the atmosphere by mesocosm respiration.

In the daytime (5:45 a.m.–7:15 p.m.), NEE represents the balance between net canopy assimilation (A_c) and soil respiration (daytime R_s). At night (7:15 p.m.–5:45 a.m.), NEE is the sum of aboveground respiration (leaf and stem respiration, R_p) and soil respiration (night-time R_s). Day-time R_s was measured in the morning (9:00–12:00 a.m.) and in the afternoon (2:00–5:00 p.m.) during each closure day at 25 locations using a LI-6200 system (LI-COR) equipped with a LI-6000-09 soil respiration chamber (LI-COR). The mean daytime R_s for each mesocosm from these measurements was used to calculate A_c from the estimated NEE on a given closure date. The nighttime R_s was not measured in this study, but was assumed to be very close to the daytime R_s since there was no significant change in diurnal soil temperature. Thus, we used the mean daytime R_s to estimate R_p from the nighttime NEE.

Statistical analyses

The differences in the nutrient contents of soils or leaves and the rates of ecosystem CO_2 exchanges (i.e., NEE, R_s, A_c, R_p) and ecosystem radiation use efficiency (RUE) between the CO_2 treatment phases or between the mesocosms (rainforest vs. desert) were tested using one-way ANOVA. For NEE, R_s, A_c, R_p, and RUE, we treated the closure days within a CO_2 treatment phase as replicates (temporal replicates). The diurnal changes in PAR, CO_2 concentration, soil temperature, and NEE were tested using two-way ANOVA (local time and CO_2 treatment phases as two dependent variables). These statistical analyses were performed using a SYSTAT 7.0 for windows (SPSS, Chicago, Ill., USA). The responses of daytime NEE to PAR and nighttime NEE to soil temperature were evaluated using the non-linear curve fitting technique of SigmaPlot (SPSS). For the NEE-PAR relationship, the Michaelis-Menten equation used here is:

$$\mathrm{NEE} = \alpha \times \mathrm{PAR} \times \mathrm{NEE_{max}}/(\alpha \times \mathrm{PAR} + \mathrm{NEE_{max}}) - R_{eco},$$

where α is the apparent quantum yield at the mesocosm level, $\mathrm{NEE_{max}}$ (μmol m^{-2} s^{-1}) is the potential NEE under the saturating PAR, and R_{eco} (μmol m^{-2} s^{-1}) is the average ecosystem respiration in the daytime.

Results

Environmental conditions during the three CO_2 treatment phases

The daily mean concentration of atmospheric CO_2 in the two mesocosms was about 900 μmol mol^{-1} for the two high CO_2 phases, significantly higher than that in the low CO_2 phase ($P < 0.001$; Fig. 2a). Over the 3-month experimental period, the daily mean PAR varied between 500 and 750 μmol m^{-2} s^{-1}, but there was no significant difference among the three different CO_2 treatment phases in either the rainforest mesocosm or the desert mesocosm (Fig. 2b). Similarly, there were no significant differences in the mean air temperature and vapor pressure deficit among the CO_2 treatment phases in the rainforest and the desert mesocosms (Fig. 2c, d).

There were no significant changes in the mesocosm nutrient contents during the entire experimental period (Table 2). Although the soils in the rainforest mesocosm contained significantly higher concentrations of major nutrients, the leaves of most common plants had no obvious differences in nutrient contents between the two mesocosms. The predawn water potentials of most common plants were relatively high in both the rainforest and the desert mesocosms, and there were no

Table 2 Means and SEs ($n = 5$) for the nutrient concentrations (on dry weight basis) in leaves and soils from the tropical rainforest and the coastal desert of Biosphere 2 at the three sampling times when the atmospheric CO_2 concentration in each mesocosm was set at high or low level in the summer of 1996. Different *superscript letters* for a nutrient among three sampling times in each mesocosm indicate significant differences at $P < 0.05$

Nutrients	Tropical rainforest			Coastal desert		
	31 May	16 June	15 July	31 May	16 June	15 July
Foliar total content						
N (%)	3.47 ± 0.33[a]	3.68 ± 0.29[a]	3.52 ± 0.29[a]	2.92 ± 0.70[a]	3.13 ± 0.52[a]	3.24 ± 0.70[a]
P (%)	0.26 ± 0.02[a]	0.32 ± 0.05[a]	0.26 ± 0.12[a]	0.33 ± 0.17[a]	0.32 ± 0.08[a]	0.23 ± 0.06[a]
K (%)	2.62 ± 0.22[a]	2.90 ± 0.71[a]	2.93 ± 0.70[a]	3.32 ± 0.24[a]	3.14 ± 1.71[a]	3.41 ± 1.58[a]
Ca (%)	1.08 ± 0.23[a]	1.26 ± 0.21[a]	1.46 ± 0.29[a]	1.38 ± 1.10[a]	1.95 ± 1.04[a]	1.76 ± 0.64[a]
Mg (%)	0.39 ± 0.08[a]	0.36 ± 0.06[a]	0.41 ± 0.07[a]	0.29 ± 0.10[a]	0.42 ± 0.24[a]	0.39 ± 0.25[a]
Fe (μg g^{-1})	203 ± 37[a]	103 ± 18[b]	72 ± 9[b]	115 ± 43[a]	74 ± 14[a,b]	60 ± 15[b]
Soil extract nutrients						
NO_3^--N 0–20 cm	11.4 ± 2.9[a]	11.0 ± 3.3[a]	8.2 ± 1.3[a]	2.8 ± 1.1[a]	2.4 ± 0.2[a]	2.9 ± 0.9[a]
PO_4^{-3}-P 0–20 cm	64.5 ± 11.5[a]	67.4 ± 10.8[a]	60.9 ± 9.8[a]	4.4 ± 1.1[a]	4.4 ± 1.4[a]	6.7 ± 3.4[a]
K^+ 0–20 cm	561 ± 127[a]	602 ± 145[a]	692 ± 162[a]	243 ± 84[a]	307 ± 103[a]	329 ± 105[a]
Fe^{+++} 0–20 cm	161 ± 27[a]	144 ± 16[a]	162 ± 17[a]	5.2 ± 1.2[a]	6.6 ± 2.2[a]	6.9 ± 0.8[a]

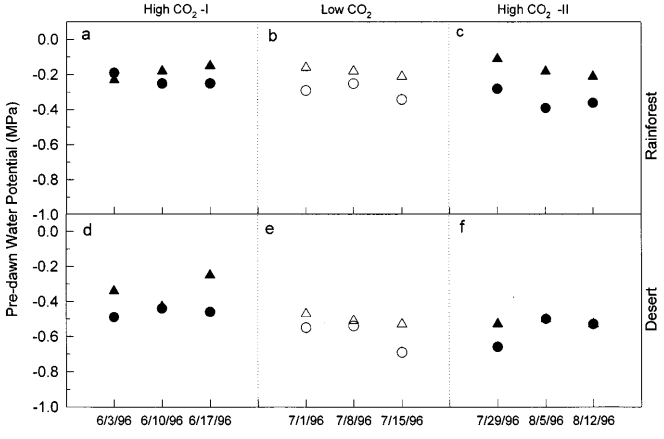

Fig. 3 Predawn water potentials for the most common woody plants in **a–c** the tropical rainforest, and **d–f** the coastal desert of Biosphere 2 during a 12-week experimental period in 1996. Each symbol represents the mean of measurements on 2–3 different species in each group

significant changes over the entire experimental period (all $P > 0.05$; Fig. 3).

Diurnal variation in PAR, CO_2, soil temperature, and NEE

In the rainforest mesocosm, PAR usually peaked around 9:00 a.m.–noon (Arizona local time) with the maximum values around 1500 μmol m^{-2} s^{-1} in all three CO_2 treatment phases (Fig. 4a–c). For the two high CO_2 phases (27 May–23 June and 22 July–15 August), the atmospheric CO_2 concentration decreased from the predawn set point (1200 ± 50 μmol mol^{-1}) to the lowest values around 4:30 p.m. (520 ± 90 μmol mol^{-1}; Fig. 4d–f). For the low CO_2 phase (24 June–21 July), the atmospheric CO_2 concentration decreased from the set points (600 ± 25 μmol mol^{-1}) to the lowest values around 4:00 p.m. (300 ± 40 μmol mol^{-1}; Fig. 4e). There was no significant diurnal change in soil temperature (Fig. 4g–i) for all closure days. The NEE of CO_2 in the rainforest mesocosm roughly followed the PAR diurnal changes, with the highest NEE in the day around 11:00 a.m. (Fig. 4j–l). The maximum NEE was about 15 μmol m^{-2} s^{-1} for the two high CO_2 treatment phases, but only about 8 μmol m^{-2} s^{-1} for the CO_2 phase. The NEE decreased slightly during the night, with the night-time NEE around 8 μmol m^{-2} s^{-1} for the two high CO_2 phases and around 6.5 μmol m^{-2} s^{-1} for the low CO_2 phase.

In the coastal desert mesocosm, PAR usually peaked around noon–3:00 p.m. (Fig. 5a–c), 2 h later than in the rainforest mesocosm. The maximum PAR values were around 1250 μmol m^{-2} s^{-1} in all three CO_2 treatment phases. The atmospheric CO_2 concentration in the coastal desert mesocosm showed similar diurnal trend to that in the rainforest mesocosm, but the magnitude of the diurnal change was much smaller (Fig. 5d–f). There was a small diurnal change in soil temperature with the highest values between 2:00 and 4:00 p.m. (Fig. 5g–i) for all closure days. The NEE showed a similar diurnal pattern to the PAR, with the highest net carbon uptake at around 2:00 p.m. (Fig. 5j–l). The daytime NEE in the first high CO_2 phase was much higher than in the low CO_2 phase and the second high CO_2 phase, while there was no obvious difference in daytime NEE between the second high CO_2 phase and the low CO_2 phase. However, the night-time NEE was significantly lower for the two high CO_2 phases than for the low CO_2 phase. In most cases, the desert mesocosm had much lower daytime and night-time NEE than the rainforest mesocosm (all $P < 0.001$).

Responses of NEE to PAR, CO_2 concentration, and soil temperature

The responses of NEE to incoming PAR at the canopy top are shown in Fig. 6 for 9 days under natural light,

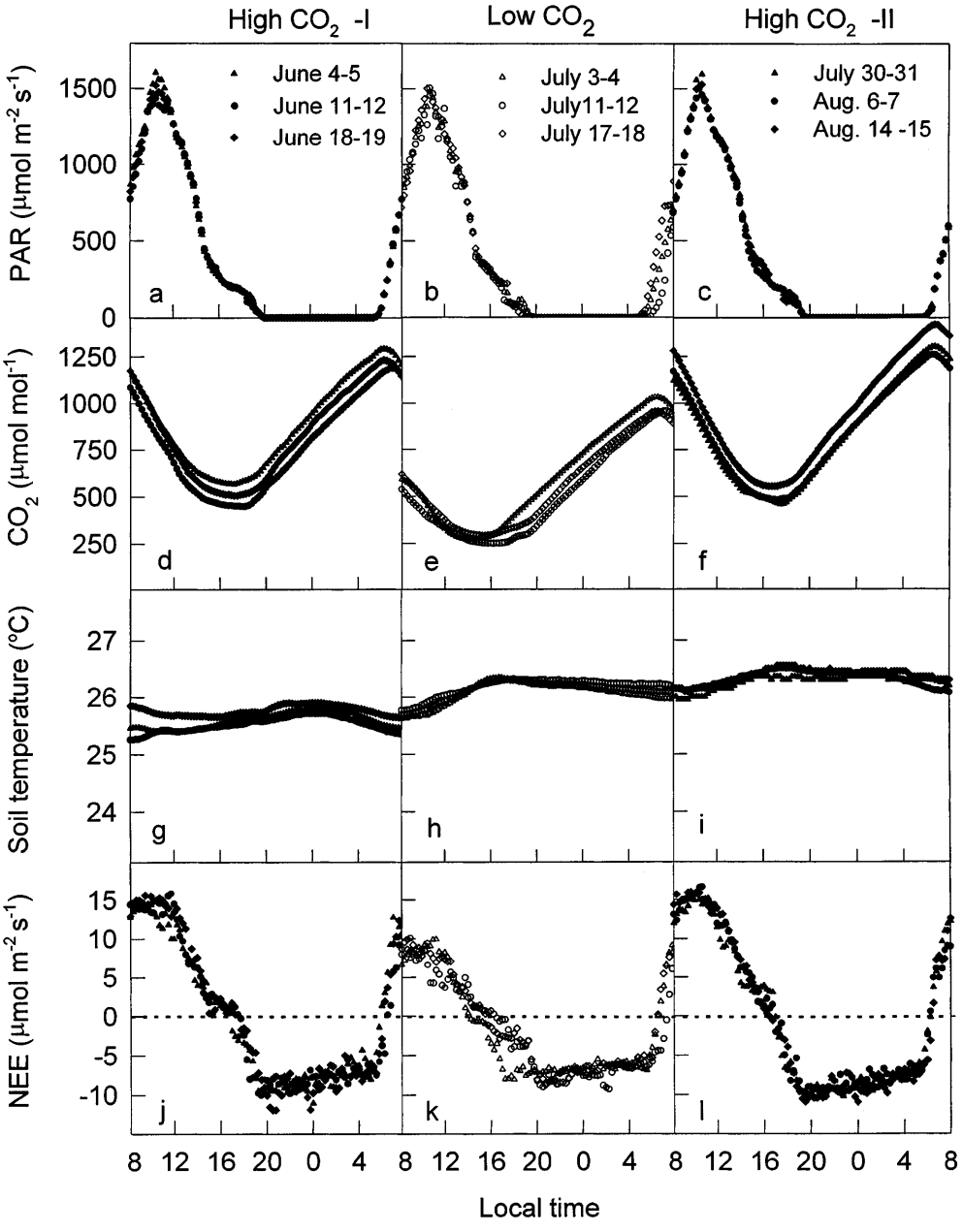

Fig. 4a–l Diurnal courses of PAR, atmospheric CO_2 concentration, soil temperature at 10 cm depth, and net ecosystem exchange (NEE) of CO_2 in the tropical rainforest of Biosphere 2 during three CO_2 treatment phases in the summer of 1996. For each CO_2 treatment phase, three diurnal courses were measured 1, 2, and 3 weeks after the CO_2 was set at a given level. Extremely low PAR occurred occasionally during daytime, resulting mostly from the shadow effect of the space frame structure. Positive NEE values indicate net uptake of atmospheric CO_2 by the mesocosm, negative values indicate net input of CO_2 to the atmosphere

CO_2, temperature, and relative humidity. The plots of observed NEE against PAR were quite scattered on all closure days, probably due in part to the variation in atmospheric CO_2. NEE in the rainforest mesocosm saturated at a PAR of around 800 μmol m^{-2} s^{-1} in all three CO_2 treatment phases (Fig. 6a–c). The ecosystem light compensation point, or the PAR level at which the mesocosm carbon uptake was balanced by the mesocosm respiration, was much lower under the high CO_2 treatments (249–253 μmol m^{-2} s^{-1}) than under the low CO_2 treatment (400 μmol m^{-2} s^{-1}) in this mesocosm. In the desert mesocosm, NEE did not increase further when the PAR was higher than 600 μmol m^{-2} s^{-1} and the ecosystem light compensation point was also higher during the low CO_2 phase than during the high CO_2 phases (220 vs. 51–129 μmol m^{-2} s^{-1}) (Fig. 6d–f). The parameters for the Michaelis-Menten fitting curves shown in Fig. 6 are summarized in Table 3.

Under saturated PAR, NEE increased from 4 μmol m^{-2} s^{-1} to 14 μmol m^{-2} s^{-1} when CO_2 concentration increased from 300 to 700 μmol mol^{-1} in the rainforest mesocosm, but did not increase further with CO_2 higher than 750 μmol mol^{-1} (Fig. 7). In the desert mesocosm, however, the data did not show that light-saturated NEE changed with CO_2 because of a large variation in the NEE under a given CO_2 concentration (not shown). At night, NEE in the rainforest mesocosm showed a significant but non-linear dependence on soil temperature (Fig. 8), while there was no correlation

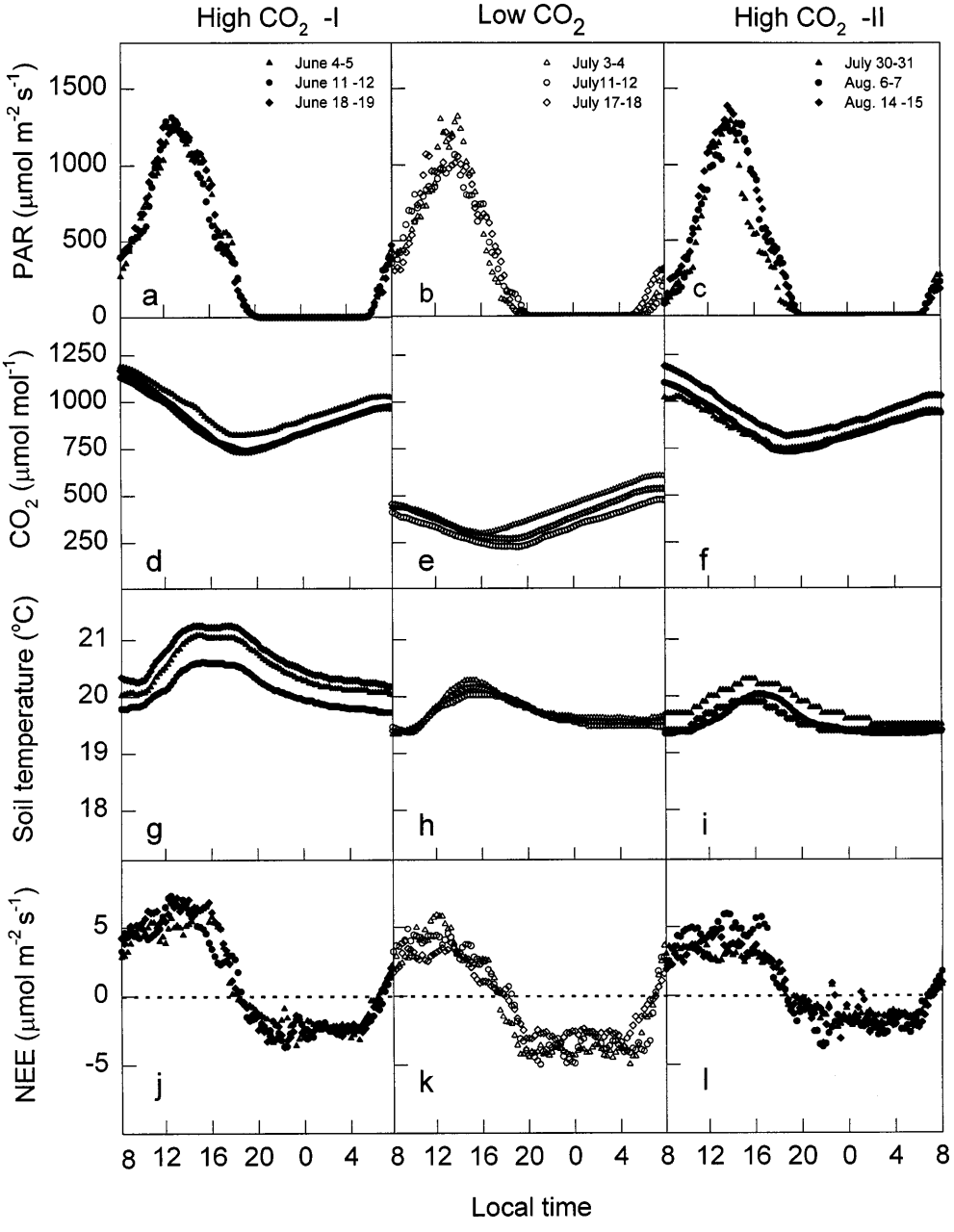

Fig. 5a–l Diurnal courses of PAR, atmospheric CO_2 concentration, soil temperature at 10 cm depth, and net ecosystem exchange (NEE) of CO_2 in the coastal desert of Biosphere 2 during three CO_2 treatment phases in the summer of 1996. For each CO_2 treatment phase, three diurnal courses were measured 1, 2, and 3 weeks after the CO_2 was set at a given level. Extremely low PAR occurred occasionally during day-time, resulting mostly from the shadow effect of the space frame structure. Positive NEE values indicate net uptake of atmospheric CO_2 by the mesocosm, negative values indicate net input of CO_2 to the atmosphere

between the night-time NEE and the soil temperature in the desert mesocosm (not shown).

Daily carbon budget in each mesocosm

Table 4 summaries the daily carbon budget for the rainforest and the desert mesocosm of Biosphere 2. The total daytime NEE was about 300 mmol m^{-2} in the two high CO_2 phases, compared to only 113 mmol m^{-2} in the low CO_2 phase. The total daytime soil respiration was about 310 mmol m^{-2} for all three CO_2 treatment phases. The daily net canopy assimilation (A_c) was significantly higher for the high CO_2 phases (about 600 mmol m^{-2}) than for the low CO_2 phase (only 427 mmol m^{-2}). As a result, the ecosystem radiation use efficiency (RUE) was significantly higher in the two high CO_2 phases (0.019, 0.018) than in the low CO_2 phase (0.013) in this mesocosm. The total night-time NEE was slightly higher in the two high CO_2 phases than in the low CO_2 phase. Although the total night-time soil respiration was almost the same for the three CO_2 treatment phases, the estimated plant respiration at night was higher for the high CO_2 phases than for the low CO_2 phase (65–82 mmol m^{-2} vs. 23 mmol m^{-2}). Over a 24-h period, this rainforest mesocosm was always a net carbon source for the atmosphere, but the strength of such source was much higher under the low CO_2 concentration than under the high CO_2 concentrations.

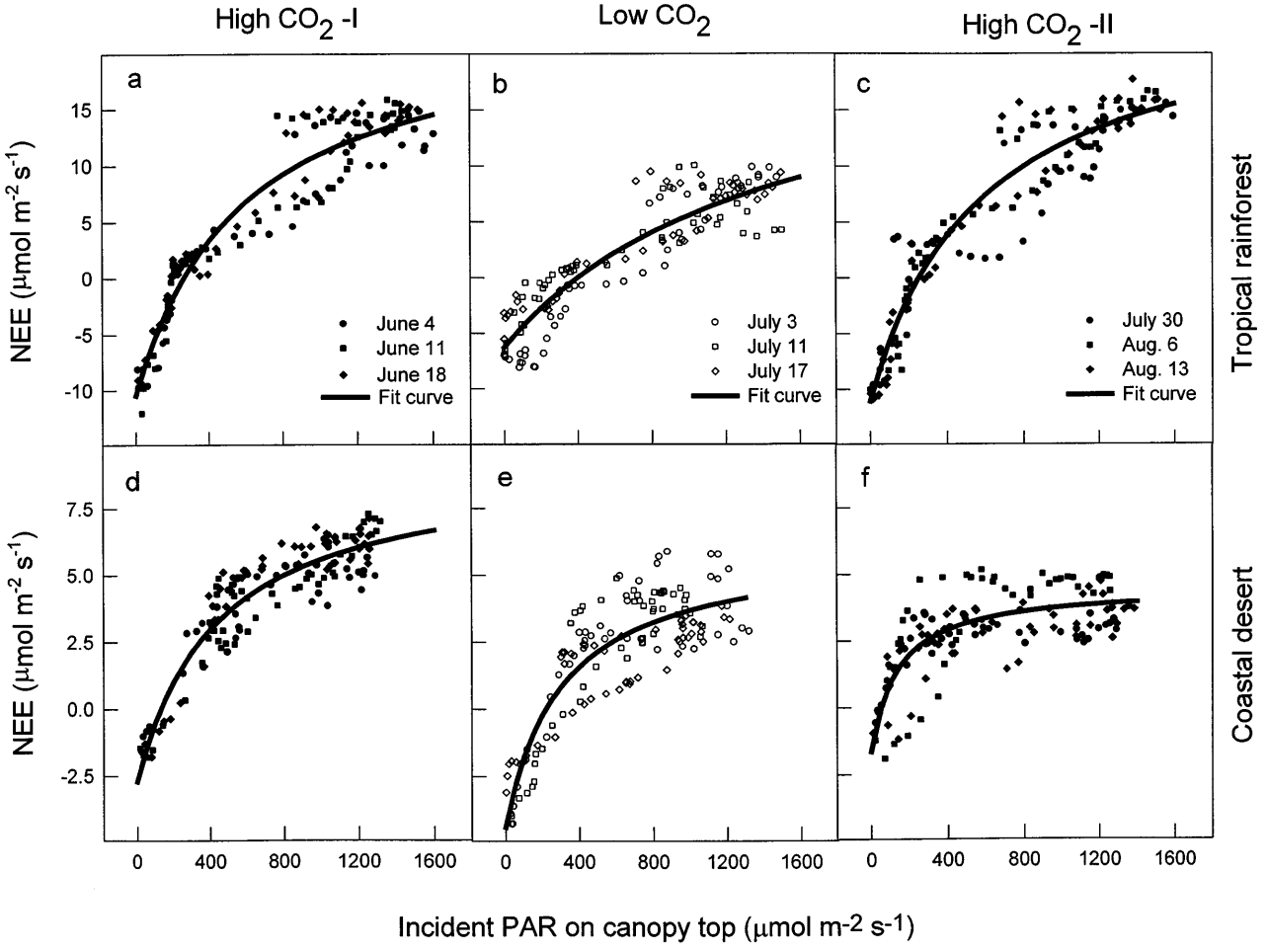

Fig. 6 Response of NEE of CO_2 to PAR in **a–c** the tropical rainforest and **d–f** the coastal desert of Biosphere 2 during the high and low CO_2 treatment phases. We expressed NEE as a positive value when the mesocosm had a net uptake of atmospheric CO_2, and as a negative value when it released CO_2 to the atmosphere. The curve in each chart was generated from the Michaelis-Menten equation: $\mathrm{NEE} = \alpha \times \mathrm{PAR} \times \mathrm{NEE}_{\max}/(\alpha \times \mathrm{PAR} - \mathrm{NEE}_{\max}) - R_{\mathrm{eco}}$, with the parameter values that best fitted with the observed data. For each CO_2 treatment phase, the data from three separate closure days were pooled for non-linear regression analyses. See Table 3 for the related parameter values

In the desert mesocosm, the daily total PAR was significantly higher for the first high CO_2 phase than for the low CO_2 and the second high CO_2 phases (Table 4). Although there was much higher daytime NEE for the two high CO_2 treatment phases than for the low CO_2 phase in this mesocosm, the difference was much smaller than that in the rainforest mesocosm. There was no significant difference in soil respiration among the three CO_2 treatment phases. The daily total A_c was higher for the first high CO_2 phase than for the low CO_2 phase and for the second high CO_2 phase, while the RUE was not significantly different among the three CO_2 treatment phases. Considerably higher A_c in the first high CO_2 phase was associated with much higher PAR during this phase (Table 3). Both the total nighttime NEE and the estimated night-time plant respiration was much higher for the low CO_2 phase than for the two high CO_2 phases, while the total night-time soil respiration was similar among the three CO_2 phases in this desert mesocosm. According to the 24-h carbon budget, this mesocosm was a net carbon source for the atmosphere during the low CO_2 phase, but changed to a net carbon sink during the two high CO_2 phases.

Discussion

Effects of elevated CO_2 on ecosystem carbon exchanges

Using the two large-scale terrestrial mesocosms of Biosphere 2, we show here that the net ecosystem carbon uptake in a tropical rainforest and a coastal desert can be enhanced by increasing atmospheric CO_2 concentration. The high CO_2 treatments also increased carbon turnover rate in the rainforest mesocosm since both the daytime and nighttime NEE were increased substantially by the high CO_2 treatments. Since there were no spatial controls and replications in this study due to the special features of Biosphere 2 mesocosms, we had to use the step-wise changes in atmospheric CO_2 concentrations

Table 3 Parameters (means and SEs) for the Michaelis-Menten equations fitted to the relationship between the observed net ecosystem exchange (NEE, μmol m^{-2} s^{-1}) of CO_2 and the incident photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) at the canopy top in the two terrestrial mesocosms of Biosphere 2 under different CO_2 treatments (shown in Fig. 6). The Michaelis-Menten equation is: $NEE = \alpha \times PAR \times NEE_{max}/(\alpha \times PAR + NEE_{max}) - R_{eco}$, where α is the apparent quantum yield at the mesocosm level, NEE_{max} (μmol m^{-2} s^{-1}) is the potential NEE under the saturating PAR, and R_{eco} (μmol m^{-2} s^{-1}) is the average ecosystem respiration in the daytime. Also shown are the correlation coefficients and the significant levels for the fitted curves in Fig. 6

Mesocosm	CO_2 treatment	α	NEE_{max}	R_{eco}	r^2
Tropical rainforest	High CO_2-I	0.058 ± 0.007	34.12 ± 1.15	10.43 ± 0.78	0.924***
	Low CO_2	0.020 ± 0.003	29.21 ± 4.41	6.28 ± 0.51	0.837***
	High CO_2-II	0.063 ± 0.008	36.06 ± 1.37	11.07 ± 0.75	0.918***
Coastal desert	High CO_2-I	0.027 ± 0.004	11.98 ± 0.43	2.70 ± 0.35	0.878***
	Low CO_2	0.034 ± 0.001	10.57 ± 0.52	4.38 ± 0.47	0.777***
	High CO_2-II	0.044 ± 0.002	6.17 ± 0.56	1.65 ± 0.65	0.584**

$^{**}P < 0.01$, $^{***}P < 0.001$

over time to examine the responses of ecosystem gas exchanges in the tropical rainforest and the coastal desert to changing CO_2. The effectiveness of this approach was reflected by the relatively small variations among three temporal replications within each CO_2 treatment phase and the remarkably high repeatability under similar CO_2 conditions (the two high CO_2 phases) for ecosystem carbon exchange rates (Figs. 4, 5).

In the rainforest mesocosm, an increase in the atmospheric CO_2 concentration from daily mean of 450 μmol mol^{-1} to 900 μmol mol^{-1} enhanced the daytime ecosystem carbon uptake by 150% and the nighttime ecosystem respiration by 15% (Fig. 4, Table 4). The desert mesocosm also showed significant enhancement in daily net carbon uptake in response to increasing CO_2 concentration through a combination of increased daytime ecosystem carbon uptake (by about 65%) and reduced night-time ecosystem respiration (by about 50%) (Fig. 5, Table 4). When the CO_2 concentration increased from about 450 to about 900 μmol mol^{-1}, the desert mesocosm changed from a net carbon source to a net carbon sink for the atmosphere (Table 4).

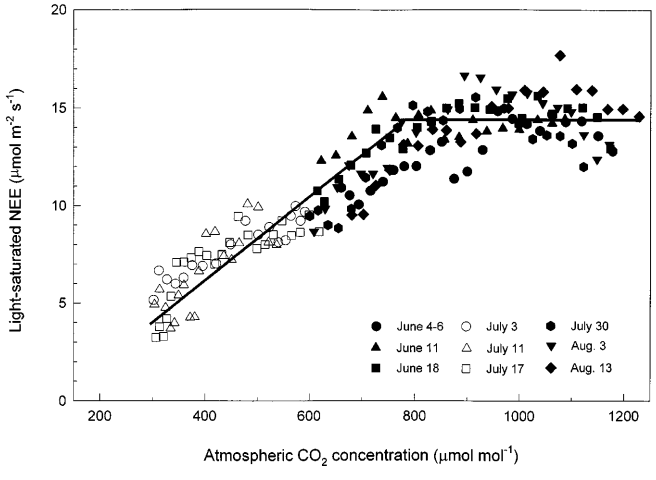

Fig. 7 Response of light-saturated NEE of CO_2 to atmospheric CO_2 concentration in the tropical rainforest and the coastal desert of Biosphere 2 during the summer of 1998. The data from all three treatment phases (*open symbols* for the low CO_2 phase, *filled symbols* for the high CO_2 phases) were pooled for each mesocosm. The *lines* were drawn by hand

During the experimental period, air temperature and relative humidity remained fairly stable for all three CO_2 treatment phases (Fig. 2). Plants in the rainforest and desert mesocosms were not under any water stress because they all had relatively high predawn water potentials (Fig. 3). The nutrient status of the mesocosms, as reflected in the foliar and soil nutrient concentrations, did not change significantly among the CO_2 treatment phases in most cases (Table 2). In addition, we conducted our experiments around the summer solstice, so canopy PAR levels were relatively high and stable throughout the 12-week experimental period (Fig. 2). Therefore, the responses in net ecosystem carbon exchanges to changing atmospheric CO_2 observed in this study should result mainly from the direct effects of elevated CO_2 on ecosystem carbon metabolism. This enhancement occurred with unlimited root volume and nutrient supplies, characteristic of soils in most mesocosms of Biosphere 2, so photosynthetic acclimation to increasing atmospheric CO_2 may not occur.

Using a smaller rainforest mesocosm, Körner and Arnone (1992) showed that increasing atmospheric CO_2 from 340 to 610 μmol mol^{-1} over 3 months had no obvious effects on net ecosystem carbon uptake or total biomass. However, they also observed that canopy carbon uptake was almost doubled and that new biomass was increased more than 20% by the elevated CO_2. In this study, we also observed that net canopy uptake increased by 40% in our rainforest mesocosm when CO_2 concentration changed from 450 to 750 μmol mol^{-1}. The higher canopy carbon uptake observed by Körner and Arnone (1992) may be a result of higher fertility in the soils they used, as reflected by relatively high nutrient release and growth rates they reported. Other previous studies with temperate agricultural, estuarine, and forest ecosystems also demonstrated such enhancement of longer term CO_2 enrichment treatment (e.g., Pinter et al. 1996; Drake et al. 1996; Owensby et al. 1996), although those with arctic or boreal ecosystems did not (e.g., Oechel et al. 1994; Hattenschwiler and Körner 1996).

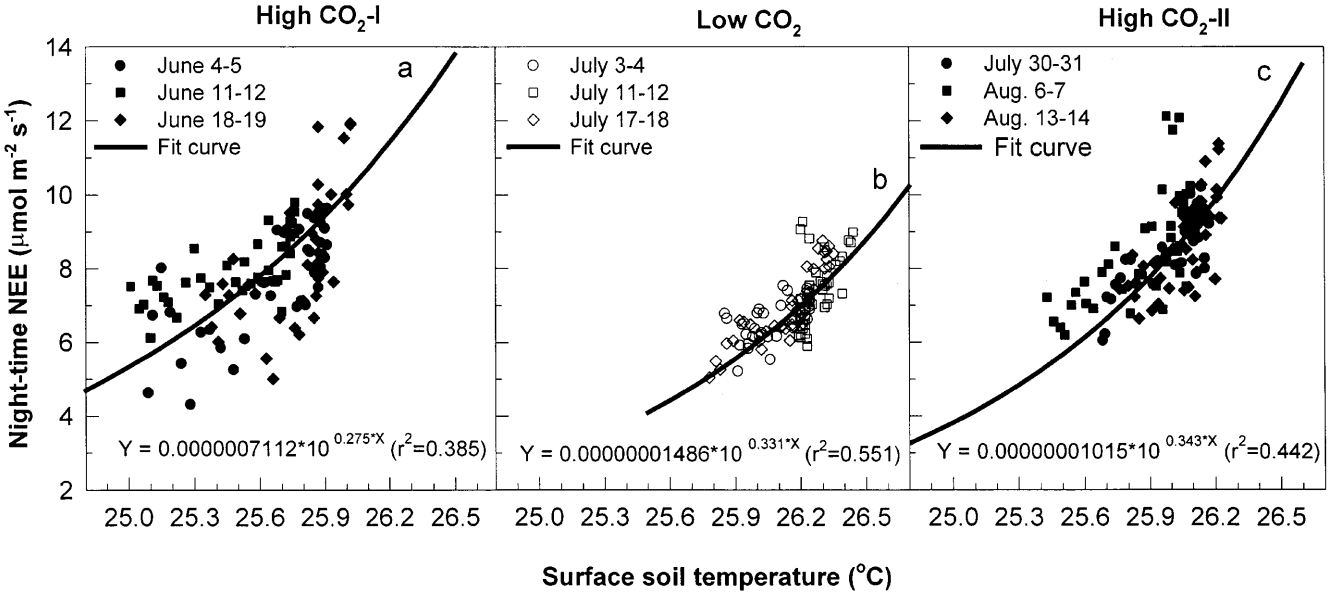

Fig. 8a–c Dependence of the night-time NEE of CO_2 on soil temperature in the tropical rainforest of Biosphere 2 during three CO_2 phases. The non-linear curve in each CO_2 phase was obtained using all data from the three closure days

Our results indicate that a short-term increase in atmospheric CO_2 concentration decreases the ecosystem light compensation point, but does not affect the ecosystem light saturation point, in both the rainforest mesocosm and the desert mesocosm (Fig. 6). Our results also indicate that, in the rainforest mesocosm, NEE showed a non-linear response to increasing atmospheric CO_2 concentration, with almost a linear increase when CO_2 changed from 300 to 750 μmol mol^{-1} but no further increase when CO_2 was higher than 750 μmol mol^{-1} (Fig. 7a). Our previous study during a winter period also observed a similar pattern, although the ecosystem CO_2 saturation point was about 600 μmol mol^{-1} (Lin et al. 1998). If this result can be applied to natural rainforest ecosystems, it may suggest that the CO_2 fertilization effect on tropical rainforest ecosystems due to anthropogenic CO_2 increase will decrease and eventually diminish when the CO_2 concentration of the earth's atmosphere reaches 750 μmol mol^{-1} sometime next century. In addition, our results echo the call of Korner (1995) for the necessity of multi-level CO_2 treatments (at least three concentrations) if one tries to predict the actual effect of increasing CO_2 concentration on ecosystem carbon exchange. Presently, most CO_2 enrichment studies adopt only two levels of CO_2 treatments, which might not be able to uncover the non-linearity of ecosystem CO_2 response as observed here for the rainforest mesocosm.

Table 4 Means and SEs (n = 3) for the net ecosystem carbon exchange (NEE) of CO_2, soil respiration (R_s), canopy net assimilation (A_c), radiation use efficiency (RUE) and plant respiration (R_p) during different CO_2 treatment phases in the tropical rainforest and the coastal desert of Biosphere 2. All values were expressed on a ground area basis. We expressed NEE and A_c as positive values when the whole ecosystem and the whole canopy had a net uptake of atmospheric CO_2. Different *superscript letters* for a parameter among three CO_2 treatment phases in each mesocosm indicate a significant difference at $P < 0.05$

	Rainforest			Desert		
	High CO_2-I	Low CO_2	High CO_2-II	High CO_2-I	Low CO_2	High CO_2-II
Daytime (5:45 a.m.–7:15 p.m.)						
Total NEE (mmol m^{-2})	296.4 ± 15.7^a	113.2 ± 19.1^b	289.7 ± 6.5^a	178.1 ± 9.1^a	94.0 ± 8.3^c	121.9 ± 16.2^b
Total R_s (mmol m^{-2})	−303.0 ± 16.8^a	−313.6 ± 14.2^a	−310.4 ± 4.1^a	−50.6 ± 11.2^a	−45.88 ± 8.7^a	−42.8 ± 16.7^a
Total A_c (mmol m^{-2})	599.4 ± 16.8^a	426.8 ± 12.3^a	599.3 ± 3.3^a	228.7 ± 12.7^a	139.8 ± 9.3^b	164.7 ± 16.3^a
RUE (mol mol^{-1})	0.018 ± 0.001^a	0.013 ± 0.001^b	0.019 ± 0.001^a	0.007 ± 0.001^a	0.005 ± 0.001^a	0.006 ± 0.001^a
Night-time (7:15 p.m.–5:45 a.m.)						
Total NEE (mmol m^{-2})	−290.6 ± 6.9^a	−256.8 ± 8.0^b	−312.2 ± 5.7^a	−86.2 ± 2.9^a	−130.5 ± 14.4^b	−61.0 ± 7.6^a
Total R_s (mmol m^{-2})	−226.8 ± 6.6^a	−233.8 ± 9.2^a	−230.7 ± 7.2^a	−37.8 ± 3.9^a	−44.0 ± 14.2^a	−41.9 ± 7.7^a
Total R_p (mmol m^{-2})	−64.8 ± 6.5^a	−23.0 ± 10.0^b	−81.5 ± 10.3^a	−48.4 ± 3.5^a	−86.5 ± 13.9^b	−29.1 ± 7.8^c
Whole day (8:00 a.m.–8:00 p.m.)						
Daily NEE (mmol m^{-2})	−5.8 ± 11.0^a	−143.6 ± 18.3^b	−22.5 ± 8.1^a	91.9 ± 7.0^a	−36.5 ± 7.6^b	61.0 ± 7.6^c

Comparison of ecosystem CO_2 responses between two terrestrial mesocosms

Multiple mesocosms within a single enclosure facility such as Biosphere 2 permit realistic comparisons of ecosystem responses to elevated CO_2 or other climate factors, since they can be subjected to similar environmental treatments. Our results indicate that, although the daily net ecosystem carbon uptake can be enhanced by increasing CO_2 in the rainforest mesocosm as well as in the desert mesocosm, the response magnitudes and components differ distinctly between them (Fig. 4 vs. Fig. 5; Tables 3, 4). The rainforest mesocosm showed a much higher absolute response in the daytime NEE to increasing atmospheric CO_2 than the desert mesocosm (Table 4). In the relative sense, the total daytime NEE was increased about 160% by the high CO_2 treatment in the rainforest mesocosm, but was only 30–89% in the desert mesocosm. However, the enhancement in A_c by the high CO_2 treatment was comparable between the two mesocosms (40% in the rainforest mesocosm vs. 18–64% in the desert mesocosm). The nighttime NEE was increased by 12–19% for the high CO_2 treatment in the rainforest mesocosm, but was reduced by about 50% in the desert mesocosm (Table 4). Since soil respiration was not significantly affected by the short-term change in atmospheric CO_2, the change in ecosystem respiration observed here resulted mainly from the response of plant dark respiration to changing atmospheric CO_2 (Table 4). Another significant difference between the rainforest and desert mesocosms in CO_2 response was the effect of elevated CO_2 on the apparent ecosystem quantum yield and the canopy RUE (Tables 3, 4). Both indexes were increased significantly by the high CO_2 treatments in the rainforest mesocosm, while they were not affected by the high CO_2 treatments in the desert mesocosm.

It is worthwhile mentioning that the less responses of the coastal desert mesocosm to increasing atmospheric CO_2 may in part result from its large proportion of C_4 plants (e.g., *Atriplex* spp., *Pennisetum ciliare*, *Panicum maximum*). It has been well demonstrated that C_4 plants are less responsive to elevated CO_2 than C_3 plants (see review by Bazzaz 1990). Thus, we can expect that, everything else being equal, an ecosystem with a considerable proportion of C_4 plants should show less response in NEE to high CO_2 than an ecosystem with only C_3 plants.

Possible errors associated with the special features of the Biosphere 2 facility

There are several possible complications in interpreting our results from this study due to some unique features of Biosphere 2 facility. First, large diurnal fluctuation in atmospheric CO_2 concentration occurs during each closure day because of the relatively small ratio of atmosphere to vegetation-soil volume in the enclosure mesocosms (Figs. 4, 5). The maximum diurnal change in atmospheric CO_2 concentration was about 600 μmol mol^{-1} in the rainforest mesocosm, and about 200 μmol mol^{-1} in the desert mesocosm. In comparison, the normal diurnal fluctuation in atmospheric CO_2 concentration in humid tropical forests is about 150–200 μmol mol^{-1} (e.g., Grace et al. 1995b) and is much less in tropical savannas (< 50 μmol mol^{-1}) (e.g., Miranda et al. 1997). Thus, plants in these mesocosms experienced CO_2 conditions that are unknown in natural habitats, which may affect the applicability of the results from this study to natural ecosystems. We are currently evaluating the possible effects of such large diurnal fluctuation in atmospheric CO_2 on ecosystem physiological processes using both experimental and model approaches. We are also installing CO_2 control systems in these mesocosms to reduce diurnal CO_2 fluctuation. Secondly, a strong thermal gradient occurred in the rainforest mesocosm because air became vertically stratified on warm sunny days in the summer. This may affect not only the calculation of ecosystem gas exchanges but also the physiological performance of the leaves in the top canopy layer. We are installing fan systems in the rainforest mesocosm to improve air mixing and reduce thermal stratification. Thirdly, our CO_2 treatment period lasted only 4 weeks for each level, so the responses of longer term processes (e.g., plant growth, biomass accumulation, litter decomposition) could not be studied. Thus, the implications of our results from this study for the natural ecosystems must be considered with caution, and be treated in the full context of the special phenomena associated with any large-scale enclosure ecosystems such as Biosphere 2. We are currently modifying these mesocosms and other sections of Biosphere 2 to have relatively constant CO_2 concentrations and to make them suitable for longer-term experiments.

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